On the Myogram of the Flexor-reflex evoked by a Single Break-shock.

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Our object has been to compare the reflex contraction of a muscle when evoked by a single induction shock with the contraction evoked from the same muscle when a similar stimulus is applied directly to the muscle's motor nerve. The experiments extend some observations previously reported in these Proceedings (2) and in the 'Journ. of Physiology' (6). The literature of the subject was given in those papers and for it reference may be had to them.

Method.

The reflex preparation employed has been the spinal cat, the muscle being tibialis anticus. Either before or after the spinal cord had been transected the animal was decerebrated. The spinal transection and the decerebration were performed under deep anæsthesia. The spinal transection was in some cases made three to ten days prior to the decerebration. The seat of spinal transection was usually at the posterior end of the thoracic region, but sometimes at the anterior end of the cervical region. All the hind-limb muscles except tibialis anticus were immobilised by nerve section, or in the case of extensores, digitorum and peronei, tenotomy. The limb was fixed by steel drills in tibia and femur, the drills being clamped to unyielding uprights on the experimental table. The tendon of tibialis anticus was attached by a short length of waxed fishing line to an isometric myograph of the torsion-wire pattern. The vibration period of this recorder was somewhat less than 0·01″. The afferent nerves of the limb were severed and those used for stimulation were popliteal in the ham, musculo-cutaneous on the dorsum of the foot, and internal saphenous, femoralis, and external cutaneous below the groin.

The break induced current used as stimulus was obtained by the automatic opening of a contact in the primary circuit. The striker opening the contact was attached to a spindle carrying the recording surface, the moment of delivery of the stimulus being thus registrable on that surface. The spindle was horizontal and rested on bearings similar to those of an Atwood machine; it was operated by the fall of a weight. After the reflexes and their latencies

had been registered the nerve of the muscle was severed and its distal stump stimulated for obtaining the motor twitch. For stimulation of the afferent nerve the break-shock kathode was placed nearer to the spinal cord, for the efferent nerve it was placed nearer to the muscle.

Results.

It will be convenient to refer to the contraction evoked by the break-shock applied to motor nerve as the neuromyal twitch.

(1) *Duration of Contraction.*—The reflex myogram was almost always of longer duration than the maximal twitch myogram. This was so even when the height of the reflex myogram was considerably less than that of the twitch (2). Often the excess in duration of the reflex contraction over the maximal twitch was great; the reflex contraction lasted sometimes even four or five times as long as the twitch contraction. The reflex contractions evoked from musculo-cutaneous nerve on the dorsum of the foot (skin) and from internal saphenous were usually of longer duration than that evoked from the popliteal, although their contraction height was less. In spite of general similarity of form the reflex from the several nerves was found to present to some extent features characteristic for the nerves severally. The prolongation of the reflex contraction lay chiefly in the prolonged subsidence of the contraction after the crest of the myogram had been reached (fig. 1).

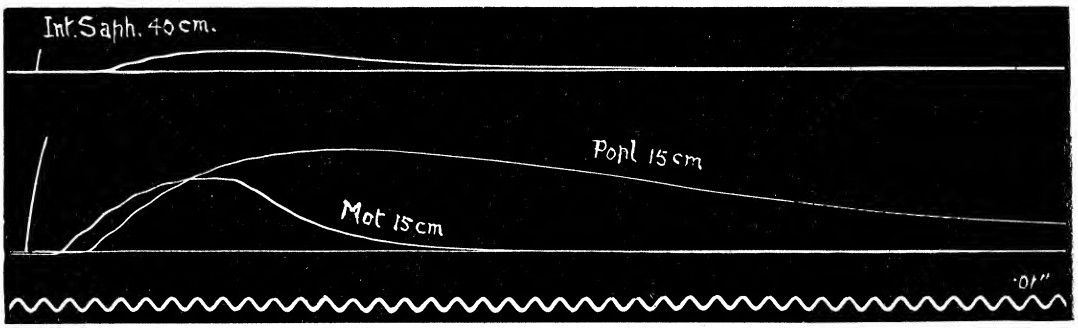

Fig. 1.—Break-shock reflexes (spinal preparation) of tibialis anticus; upper line, internal saphaneous nerve stimulated with secondary coil at 40 cm. from primary; lower line, popliteal nerve stimulated, coil at 15 cm., and, for comparison, a maximal twitch contraction given by stimulating motor nerve (peroneal) with coil at 15 cm. (break-shock). Time in 0·01″.

(2) *Crest-height.*—With the isometric myograph the height of the myogram is an index of the degree of tension developed by the contraction. In the reflex contractions the tension crest was reached relatively later after onset of the contraction than in the neuromyal twitch. In most of our preparations

a reflex crest-height could be obtained exceeding that of the maximal neuromyal twitch (2) (6), and with the secondary coil no nearer to the primary for the reflex than for the twitch. To obtain this excess of contraction height above that of maximal twitch the stimulus had always to be much above threshold (4) (7). Under successive increase of the induction-shock stimulus the successive increase of the reflex contraction (flexor) runs a course different from that of the neuromyal twitch. In the latter, as is well known, the maximal twitch is reached soon and then remains constant throughout a long range of further increment of stimulus (maximal stimuli). In the reflex the contraction goes on increasing through a far longer range of stimulus increments; it is in the upper part of this series that the reflex contraction exceeds the maximal twitch. The result was obtained from any one of the afferent nerves used for the reflex, but most readily from the largest of them, the popliteal in the ham. That the superiority of the height of the contraction excited with the electrodes on the afferent nerve was not due to escape of the current to the motor nerve or muscle, thus adding a twitch contraction to the reflex, was shown by the latent interval of the response remaining of characteristic reflex length (fig. 2).

(3) *Steepness of Ascent.*—The ascent of the myogram of the reflex contraction is not unfrequently for part of its course more steep than is any part of the ascent of the maximal twitch. This tends to occur especially when the crest-height of the reflex is greater than that of the maximal twitch.

(4) *Abruptness of Contraction.*—In the myogram of the maximal neuromyal twitch, the vibrations of the recording lever are more evident than in the myogram of the reflex contraction, an indication that the first onset of the pull on the lever is more abrupt in the twitch contraction than in the reflex contraction. Forbes and Gregg (3) pointed out that, in their galvanometric records of the action-current of the motor nerve, the rise of the current was of sharper development with motor-nerve stimulation than with reflex stimulation. In some experiments we transected the cord several days before the myographic examination. We thought thus to favour the freedom of the flexor reflex by allowing time for subsidence of spinal shock. We found, however, that when a week or more—our longest period was fourteen days—is allowed to elapse after the spinal transection, change ensues in the nerve-muscle preparation itself. The maximal twitch of tibialis anticus, in response to a break-shock applied to its motor nerve, is then feeble and sluggish, of low crest-height, and of abnormally prolonged decline. The duration of the twitch may then be twice or thrice the normal. And in this condition, the reflex contractions, as elicited by a single-shock from afferent nerve or skin, are poor and sluggish, their crest-height

seemingly even lower than can be accounted for wholly by the impaired state of the peripheral nerve-muscle apparatus itself. The wasting of the limb-musculature is also very obvious. The condition was clearly less favourable for the observations we had in view than that obtaining in the earlier periods after the transection.

Discussion of Results.—1. In the assemblage of striped fibres composing a muscle, the modes of summation of their contraction are of course two. One of these is that exemplified in the twitch contraction. There, in each of some or all of the component fibres of the muscle, a single wave of contraction is generated; the occurrence of this wave is practically simultaneous in all the contracting fibres. These individual mechanical tensions of the several component fibres of the muscle sum additively; the tension developed by the muscle, as a whole, gives the resultant tension of this single-wave contraction. The upper limit of the tension-effect of this summation of a single-wave contraction, coincident in time in the individual fibres of the muscle, can be found for a given muscle from the isometric record of its maximal twitch. Where the given muscle develops a tension superior to that developed in its maximal twitch, there must be at play, above and beyond summation of the above kind, some amount of that other well-known mode of summation due to fusion of successive contraction-waves ensuing within the self-same individual fibres of the muscle. We may for brevity distinguish these two kinds of summation as "fibre summation" and "wave summation" respectively.

Applying this to the above-mentioned result, namely, to the excess of crest-height observed in the reflex contraction as contrasted with the maximal twitch when the former is excited by a break-shock of considerably above threshold value, yet not greater than that used for the compared maximal twitch, we infer that there is in the reflex contraction a factor of wave-summation in addition to the fibre-summation. That is, a single break-shock stimulus, which evokes in the neuromyal preparation a single wave contraction, evokes when applied to the afferent nerve a succession of contraction waves, at least in some of the fibres of the muscle.

2. A possible reason for this might be that a proprioceptive reflex, initiated by the contracting muscle itself, appended itself to the reflex contraction evoked by the extrinsic afferent nerve. In the spinal preparation, a proprioceptive reflex is easily elicited from tibialis anticus (Asayama) (1), *e.g.*, by a brief pluck upon the severed tendon of the muscle. We therefore proceeded to observations in which the afferent nerve-fibres from the muscle had been severed from their connections with the spinal cord. The afferent nerve-fibres from tibialis anticus, and, indeed, from all the pre-tibial and post-

tibial crural and pedal muscles pass to the spinal cord *viâ* the ipsilateral dorsal roots of the 6th, 7th, 8th, and sometimes 9th post-thoracic spinal nerves (5). Severance of these roots leaves still open for reflex play upon the muscle several important afferent nerves of the limb, namely, internal saphenous, femoralis, and external cutaneous. The two former will have lost some of their afferent fibres, but will yet retain, as experience showed, enough to evoke extensive reflexes. The motor nerve-fibres to tibialis are, of course, untouched by the severance.

Our procedure has been to cut, with full aseptic precautions and under deep anæsthesia, the dorsal roots of the 6th, 7th, 8th, and 9th post-thoracic nerves of one side, then a few days later to sever the cord aseptically at the 12th thoracic segment, and finally a few days later to decerebrate and proceed in the same manner as before to the myographic observations of the reflex and neuromyal contractions. As afferent nerves employed for evoking the reflexes, our choice was, of course, limited to internal saphenous, femoralis, and external cutaneous. By femoralis nerve is meant the whole anterior crural trunk except internal saphenous. It includes, therefore, the afferent nerve fibres from the quadriceps, extensor muscles, etc. Our observations found that the break-shock reflexes elicited showed still (figs. 2 and 3) the character of being, when the break-shock was of considerably above threshold value, both longer and of greater crest-height than the maximal twitch elicited by a similar stimulus applied to motor nerve itself. That the afferent arc of tibialis anticus, etc., had been broken was guaranteed in each experiment in several ways. For instance, by trial to obtain the proprioceptive reflex of the muscle, this reflex proving to be inelicitable in each case, though easily provocable in the contralateral limb. Also by *post-mortem* examination of the spinal roots in the vertebral canal, which showed that the roots severed had been those required: in two cases the posterior half of the 5th root had been cut as well. Also by inability to provoke by any means any reflexes from the peroneal or popliteal nerves. The knee-jerk was also entirely absent in three cases and extremely slight in two others. But as regards the crest-height and duration of the break-shock reflex elicitable in tibialis anticus, these remained often, when the stimulus was considerably above threshold strength, superior to those of the maximal motor twitch-contraction. We obtained, therefore, no support for the supposition that that superiority was founded on combination of the break-shock reflex evoked from the extrinsic afferent with a proprioceptive reflex initiated reflexly in the contracting muscle itself.

3. That the reflex contraction develops more than one single contraction-wave (per fibre) is evidenced not only by the excess of crest-height above

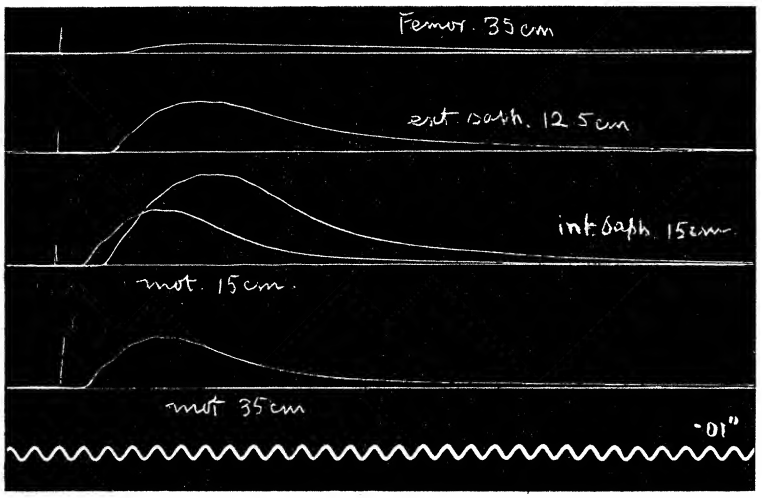

FIG. 2.—De-afferented tibialis anticus (spinal preparation); top line, reflex response to break-shock, coil at 35 cm. applied to central end of femoral nerve; second line from top, reflex to break-shock, coil at 12·5 cm., applied to external cutan-nerve; third line from top, reflex to break-shock, coil at 15 cm., applied to central end of internal saphenous nerve; and maximal twitch from break-shock, coil at 15 cm. applied to peroneal nerve; bottom line shows that twitch is already maximal under break-shock with coil at 34 cm. Time in 0·01".

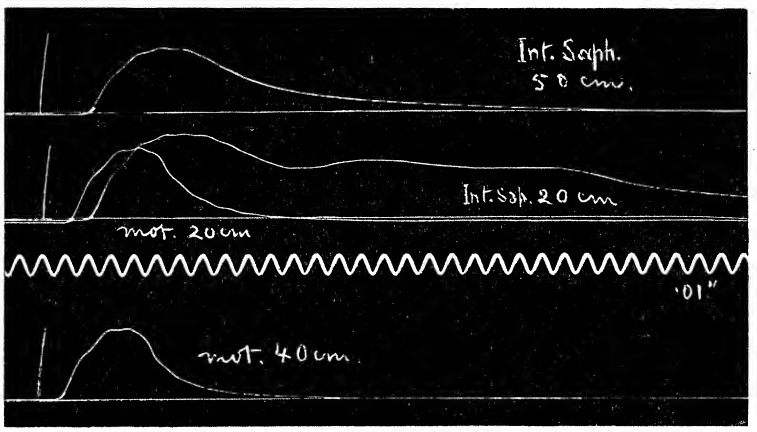

FIG. 3.—De-afferented tibialis anticus (spinal preparation); top line, reflex to break-shock, coil at 50 cm. applied to internal saphenous nerve; second line, similar but with coil at 20 cm., a maximal twitch is given for comparison with coil at 20 cm. and stimulus of motor (peroneal) nerves; bottom line, a twitch with motor nerve stimulation (break-shock) at 40 cm., showing that twitch is already maximal. Time in 0·01".

that of the maximal twitch, but also by several other features of the myogram. (1) The excess, often very great, of the duration of the reflex contraction. It may persist for several times as long as does the maximal twitch. (2) The incidence of the crest of the contraction, also when that crest-height exceeds that of the maximal twitch, falls later after onset of contraction in the reflex than in the twitch. (3) In the reflex contraction there not infrequently ensues after the main crest a second, or even a third contraction-crest, breaking the line of subsidence of the reflex, and of period far too slow to be referable to the vibration-period of the recording apparatus. (4) The ascent of the reflex myogram is sometimes in part of its course more steep than is any part of that of the maximal twitch; this is difficult to understand except as due to summation of repetitive contraction-waves in individual muscle-fibres. It sometimes occurs as early as the 15th σ in the course of the contraction.

4. Reflex contraction of tibialis anticus is readily elicitable by a single induction shock applied to the skin of the limb, *e.g.*, to the skin of the foot. We have compared the isometric myograms of this reflex contraction (fig. 4) with the maximal twitch evoked in the same preparation from the motor nerves.

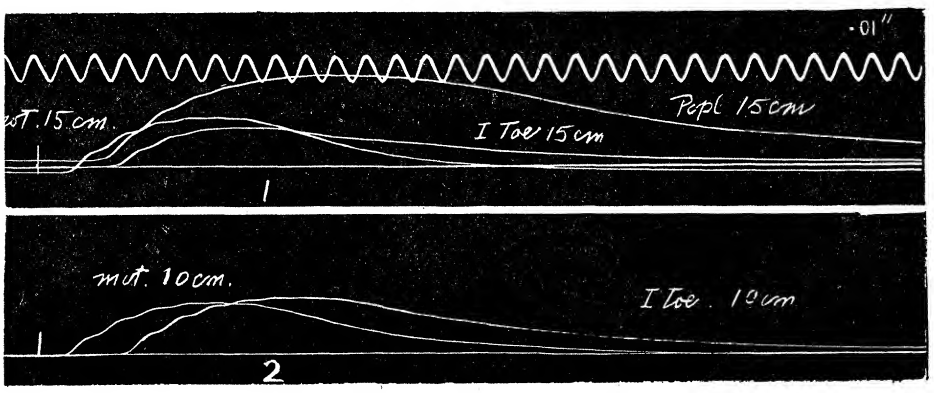

Fig. 4.—Reflex contractions of tibialis anticus (spinal preparation) in response to single break-shock applied to skin (unipolar); top line, three myograms given by break-shock, coil at 15 cm., applied respectively to skin of first digit, to central end of popliteal nerve, and to distal end of peroneal nerve (maximal twitch); bottom line, reflex from skin of first toe, coil at 10 cm. compared with motor nerve stimulation also at 10 cm., *i.e.*, maximal twitch. Time in 0·01″.

To evoke the reflex the break-shock was applied as follows: A broad copper plate was fastened to the sole of one forefoot, a layer of cotton-wool soaked in strong salt solution intervening between the skin and the plate. For the stigmatic electrode the point of a small entomological gilt pin, attached to

very thin wire, was inserted a millimetre or less into the skin of the dorsum of one of the hind toes, and the wire brought to one binding screw of the short circuit key of the secondary circuit, the wire from the copper plate being brought to the other binding screw of the key. The stigmatic electrode was made the kathode for the break-shock. The registration, etc., was as in other experiments.

The myograph records showed that, with break-shocks considerably above threshold value, the reflex contraction was often of greater crest-height, as well as of longer duration, than was the maximal twitch contraction evoked from the motor nerve. The myogram of the break-shock reflex elicited from the skin resembled that of the break-shock reflex evoked from the bared skin nerve, *e.g.*, musculocutaneous nerve, except that the skin reflex tended to be somewhat less prolonged.

5. In the spinal preparation, reflex contraction of tibialis anticus and other flexor muscles of the limb is obtained from the ipsilateral afferent limb nerves more readily than in the decerebrate preparations (7), and the reflex contraction is more ample. In some of our experiments, we have taken myograms of the tibialis anticus break-shock reflex in the decerebrate condition, and then in the spinal condition, the spinal transection being made either in the posterior thoracic region or in the anterior cervical. Both with the low and the high spinal transection, the difference between the decerebrate reflex and the spinal has been great (fig. 5). Very rarely has the crest-height of the decerebrate reflex equalled that of the maximal twitch evoked *vid* motor nerve. Often it has been less than half of that even with break-shocks much higher on the inductorium scale than those sufficing for the maximal twitch. In our experience, the break-shock reflex contraction of tibialis anticus evoked from even the popliteal nerve in the decerebrate condition gives a low relatively flat myogram of rather prolonged duration, longer usually than that of the maximal twitch. The reflex provoked from the same afferent nerve, and by a similar stimulus in the spinal preparation, may have a crest-height four or five times that of the decerebrate reflex (6),(7). This greater reflex response in the spinal, as compared with the decerebrate preparation, is obvious immediately, *e.g.*, ten minutes after spinal transection. That it is, however, a release phenomenon rather than merely an irritative excitation from the fresh trauma, is indicated by its persistence, not only for many hours but for some days, to judge from the similar character of the reflexes obtainable, when the cord had been cut, as in some of our experiments, a week or more prior to the myographic examination. Also, the threshold value of stimulus (break-shock) is higher, often far higher, in the decerebrate (6), (7), than in the spinal condition (6), (7). Also, the upper

stage of the grading of reflex response to a single-shock is, with the flexor muscle, much less extensive in the decerebrate than in the spinal preparation.

6. To summarise, we find that in the spinal preparation a single break-

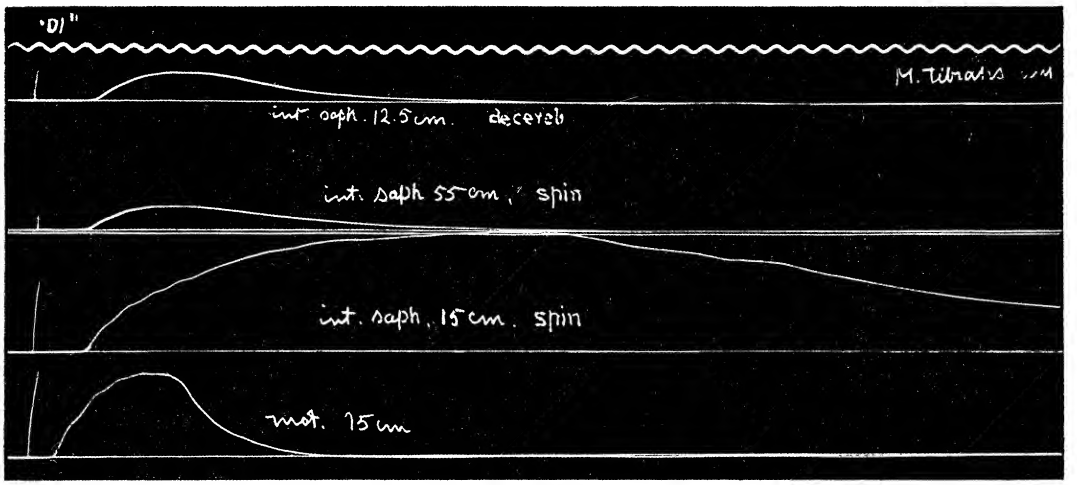

FIG. 5.—Reflex contraction of tibialis anticus in response to single break-shock stimulus of afferent nerve trunk compared in the decerebrate (top line) and spinal (second and third lines from top) conditions respectively, and with a maximal twitch from motor nerve (bottom line); the coil at 12·5 cm. in the top line, and at 15 cm. in third and bottom line; at 55 cm. in the second line from top. Time in 0·01".

shock, whether applied to a bared afferent nerve or to local skin, evokes when the shock is considerably above threshold value a reflex contraction which is both stronger and more prolonged than is the maximal twitch evoked from the motor nerve itself, and that this is so whether or no the muscle retains its own intrinsic proprioceptive reflex arc. This excess of the reflex contraction over the maximal twitch indicates that summation of successive contraction-waves is present in the reflex contraction. So, further, does the occurrence, not unfrequent, of a more rapid up-gradient of tension development, despite less abrupt first onset of tension development, in the reflex than in the maximal twitch. In other words repetitive discharge from the reflex centre occurs in response to a single induction shock stimulus applied to an afferent nerve or to local skin connected with that centre.

It may be that the stimulus applied to the afferent nerve or to the skin sets up a local change which, before it subsides, originates there not merely one but a short series of nerve impulses. We are examining this possibility further. If it be so it is remarkable that the similar stimulus supplied to the

motor nerve excites there not a repetitive series of impulses but (per fibre) one single impulse only, evoking a twitch contraction, not in a tetanic contraction.

On the other hand, it may be that the spinal reflex centre on receipt of a single-impulse volley from the afferent nerve responds by an impulse-discharge repetitive in character. Such a result might be due to the impingement upon the centre's cells severally of numbers of terminals coming from the afferent path, so that upon any one central neurone there converged a number of excitatory impulses, some arriving later than others. Or it may be that across the central path of the reflex there is some structure, *e.g.*, a synaptic membrane, which has a property of repetitive activity in result of, or in response to, the arrival at it of even a single impulse or of a single simultaneous set of impulses.

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